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ANIMAL LIGHT, WITH SPECIAL REFERENCE TO THE
SYNCHRONOUS FLASHING OF FIREFLIES.

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In one of the early numbers of the Journal of the Natural History Society there appeared an article on fireflies and glow-worms in which the author, Mr. K. O. Blair (1), discussed the phenomenon of luminescence quite completely from the natural history standpoint. To review this phase of the subject would be a needless repetition, and so it is the intention of the present writer to discuss some of the work which has been done on the physiology of luminescence.

From the earliest times the flashing of fireflies, the shining of dead flesh and decaying wood, and the phosphorescence of the sea has occasioned wonder among those people who have observed the phenomena. How light could exist without an appreciable amount of heat appears almost paradoxical, but when one studies the chemistry of living light it is quite evident that here is a reaction belonging to the large group of luminescent chemical processes requiring oxygen for their completion, and known as *oxidations*. In fact, this property of luminescence, its total dependency upon a supply of oxygen, was one of the first to be recognized. By a series of rather ingenious experiments, Robert Boyle (2) was able to demonstrate how vital a part the oxygen of the air played in this phenomenon. Taking a piece of shining wood and a live coal, he placed both under a bell-jar and exhausted the air. He found that the light in both

the coal and the piece of wood was extinguished, but, upon the readmission of air to the jar, the wood regained its light whereas the coal remained quite dark. He very naturally concluded that both the fire in the coal and the light of the wood were reactions depending on a supply of air, but that the agent producing the luminescence of wood was quite different from the fire of the coal, inasmuch as it was able to appear upon the admission of air. Of course, Robert Boyle did not know that the shining of the wood was a phenomenon connected with living processes for it was not until two hundred years later that Heller (3) was able to identify the organism responsible for the light and place it among the Fungi. Subsequent research has shown that all luminescence of damp wood is caused by fungi, for the most part by the mycelium of the plant, although in some cases the fruiting parts are also concerned.

Another rather interesting observation on the light of plants is in connection with medicine. Before the days of antiseptic surgery for soldiers wounded in battle, it was rather frequently noted that the wounds became more or less luminescent after a time. This was considered a very good sign for invariably they healed without further complications. However, it was not until late in the 19th Century that the causative agent of this luminescence was discovered. To Heller (4), again, belongs the credit of being the first to identify bacteria as the organisms responsible for the shining of flesh, and now we know that all of the luminescence of flesh is due to some member of this group of minute plants.

To people traveling on the tropical seas, the light given off by the water when it is disturbed by the passage of a boat is always a sight to arouse their admiration and wonder. This phenomenon is generally spoken of as the "phosphorescence of the sea"[†]. In this

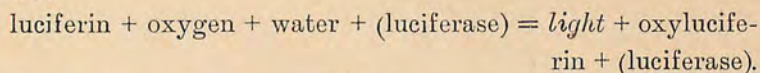
[†] The use of the word "phosphorescence" in this connection is quite misleading. There is a technical meaning for that word which has no bearing whatever on the phenomenon of the light of the sea. Strictly speaking, the word should only be used to describe a *physical* phenomenon occurring within certain atoms under very particular conditions of excitation, and is not to be confused with either the slow oxidation of phosphorous which is accompanied by light, or with the production of light by animals and plants.

instance, as with the wood and the flesh, the luminescence of the sea is due to the presence of various forms of life. The strong flashes of light which one frequently sees in the wake of the vessels may be due to the presence of either luminescent comb-jellies (Ctenophores) or jelly-fish (Medusae), while the steadier and more wide-spread light is due to a large number of microscopic one-celled animals, the Dinoflagellata. The passage of the boat through the water with its attendant light brings up another physiological property of luminescent forms. It is a general rule that it is necessary to stimulate animals in some manner before there is a production of light, whereas plants give off a continuous glow. However, aside from this point, there is no difference between the light produced by animals and that of plants.

One of the most important steps in the study of luminescence was taken by Spallanzani (5). He found that it was possible to remove luminescent forms from the sea and, by drying them rapidly, use them as material for later studies. Not only does this greatly facilitate the handling of luminescent material so that a quite comprehensive study of the chemical and physical properties has been possible, but it also brought out another point with regard to their physiology. This dried material was non-luminescent as long as moisture was kept away from it, but as soon as water was allowed to come in contact with it, the substances became as brightly luminescent as in the natural state. This pointed to the fact that in the animals at the moment of light production the photogenic substances were in the form of an aqueous solution.

Comparatively recent researches by Dubois (6) and Harvey (7) have made quite evident the reactions which proceed in an animal or plant's body. It has been found that the photogenic processes are very similar to other oxidations carried on by living organisms. There is present a specific protein substance which unites with oxygen, and it is during this process that light is produced. This substance, *luciferin*, however, can be oxidized with photogenesis only in the presence of a specific enzyme, *luciferase*. The luciferase does not unite with the luciferin, but rather plays the part of a substance which hastens the reaction, a catalyst. If one were to write a very general chemical equation for this process, it would appear somewhat

as follows :



Oxyluciferin is the product obtained on the oxidation of luciferin, and it is during this process that light is evolved. In the animal's body the oxyluciferin can be reduced back into luciferin, and it is thought that the reduction, or loss of oxygen, is accomplished by the action of an enzyme possibly closely related to luciferase. Thus a luminescent form has not only the power of forming the original substance out of the protoplasm of its cells, but it can also utilize the products of the reaction in a most economical manner.

Taken from a purely chemical standpoint, the name which can be given to this form of light production is *bio-oxo-chemo-luminescence*, or the light produced by living organisms is in the form of a chemical oxidation.

Now to turn to the physical side of luminescence. The radiations given off by luminescent plants or animals differ only slightly from those † produced by non-living light sources. True, the entire absence of heat places it apart from the great majority of luminescent phenomena, but even in this respect it is not without a counterpart, for other similar phenomena are known. The rubbing together of crystals, the luminescence of certain compounds when excited by radio-active substances, and the light emitted by the skin, lens of the eye, and teeth when struck by ultra-violet radiations are all examples of "cold light." In fact, this name may be applied to any luminous radiations emanating from a body, the temperature of which is below that necessary to make steel glow—about six hundred and sixty-five degrees Centigrade. Above this temperature, the name "incandescence" is usually given to the production of light by a body.

There is a general rule that as a substance is heated the spectrum of the radiations increases on either side of the region of the visible rays. The portion of the spectrum containing the wavelengths which are too long to produce the sensation of sight when they strike the retina of the eye are known as the "infra-red" rays

† Harvey (8) has found that less than one-tenthousandth of a degree Centigrade is liberated during this process.

while the corresponding short-wave-lengths are the "ultra-violet" radiations. Both of these groups of emanations have a very marked effect on living protoplasm, the former having a heating effect, while the latter are chemical in their action. Neither of these, for quite obvious reasons, appear in the spectrum of the light of the firefly, or any other luminous animal or plant.

The absence of these two groups of wave-lengths is of considerable theoretical importance. It means that the energy required for the production of light is almost completely converted into a visible form, only a minute amount being needed for the combination of the substances, and none being wasted in the formation of invisible radiations. Thus, Coblentz (9) found that the firefly is a 92% efficient source of light when one takes into consideration the theoretical amount of energy produced by a given amount of food material. The firefly, at least, is far more efficient and economical in its production of light than any man-made source of visible radiations. Although other luminescent forms have not been studied with the same intensity as the firefly, it would not be amiss to ascribe to them similar properties, inasmuch as they possess the same photogenic substances.

To those who are interested in the natural history of Siam, there is undoubtedly no more thrilling a sight than to see whole stretches of the canal or river bank alternately lit up and plunged into darkness by the flashing of myriads of fireflies. This phenomenon, however, is not unique to Siam, but may be found in various places throughout the Far Eastern tropics: in Burma, Malaya, Southern India, the Philippines, and elsewhere. Moreover, from parts of Italy and America have come reports of occurrences of a somewhat similar nature, but whether this can be said to be the same as the synchronism found here is a question, since, in the first place, it is of rather infrequent occurrence in both Italy and America, and, secondly, the persons who have observed the synchronism in these places apparently have never seen the phenomenon as it is found out here.

In common with the great majority of luminescent forms, fireflies have a special organ, or series of organs, in which the luciferin and luciferase are elaborated, and in the vicinity of which

photogenesis takes place. Among the insects this production of light is very intimately connected with their method of respiration. In these animals we find that breathings is accomplished by means of a series of lateral openings called the *spiracles*. Tubes running from these carry air through all parts of the body directly to the cells, thereby eliminating, to a great degree, the respiratory function of the blood. These tubes, the *tracheae*, not only regulate the amount of air passing into the animal's body, but also tend to keep out the dust and dirt which otherwise would be drawn in.

Among the fireflies, each photogenic organ is supplied by two large tracheal trunks which meet and anastomose from the two opposite sides of the abdominal segment, and give off in their length secondary branches, the *tracheal units*.

These tracheal units then approach the light mass and either deploy on its upper surface, or enter and pass into and between the cells. Finally they give off a large number of *terminal twigs*, each of which ends in an *end cell*, and beyond this are further prolonged into several fine branches which reach out and between the cells which they are to supply with air. These fine branches have been given the name of *tracheoles*, and it is in them that the production of light takes place.

From the histological standpoint, the photogenic organ consists of two kinds of cells, one above the other. The upper of the two layers is filled with fine crystals which act as a reflector for the light produced by the lower layer of cells. This lower, or external, layer is protected on the outside by a thin layer of chitin which, however, is not modified to form a lens as is the case in some of the shrimps. Between the various cells which make up this lower layer of the photogenic organ pass the tracheoles, and into these is secreted the light-producing materials in the form of a fluid. When this material comes in contact with the air in the tracheoles, there is a flash of light which is reflected to the exterior by the crystalline layer behind it.

Although the literature on the synchronous flashing of fireflies is meagre when compared with that on some other biological phenomena, it is, nevertheless, fairly copious. Through the courtesy of Dr. Hugh M. Smith of the Department of Fisheries, I have been

able to review a great deal of it, and select some of the more important theories which have been advanced to explain this unusual sight. Many of the articles have been written by travellers who have visited Siam and the Malay Peninsula and have seen the synchronism only once or twice. The result is that their observations will not stand a careful review. To give a formal review of all of these papers would be quite outside of the scope of this paper, and furthermore, a needless repetition of the papers by Professors Gudger (10) and Morse (11), so it is the intention of the writer to merely mention some of the theories and point out how they fit the observed conditions.

In general, there are five points which should receive special attention: (1) Practically all of the writers both of the many popular and few scientific articles, mention the fact that one sees the fireflies congregated on small trees either along the banks of a stream or in low swampy ground, and furthermore, as Sir John Bowering puts it, "they have their favourite trees" (12). (2) Perhaps the most popular theory to explain the synchronism is that of "sympathy." According to this idea there is some particular insect which acts as a pace-maker for all of the rest of the flies on a tree, and they follow him, regulating their flashes by his, the tempo being taken up by adjoining trees until whole stretches are in unison. (3) The second most popular theory deals with the effect slight currents of wind have on the animals. It is held that the body of the animal is slightly tilted from one side to the other, alternately exposing and hiding the luminous organs. (4) To some, the rhythmical breathing of the animals explains why all should flash in unison, the flash, according to these observers, appearing when the air is taken into the body, and darkness following on the expulsion of the air. (5) Finally, Mr. K. O. Blair (13) makes the statement that the true synchronism is not found among animals outside of the Oriental Region.

When one makes any observations of a serious nature on the synchronous flashing of fireflies, he is at once impressed by the fact that they are scattered all over a tree, some on the upper surface of the leaves, and others on the lower surface, and, around Bangkok, one finds them without exception, congregated on the trees of the species *Sonneratia acida* (the "ton lampoo" of the Siamese). This

condition of their being so generally scattered over a tree excludes, with one possibility which will be mentioned later, the synchronism being occasioned by a "pace-maker" and subsequent "follow-the-leader" action on the part of the flies. In fact, it is quite impossible for such an action to be the case, inasmuch as all of the animals are not within sight of any one particular insect, and should there be a pace-maker, there would be a wave of light passing over the tree instead of the separate and distinct flashes which one sees†. This wave would be occasioned by the transmission of the signal from one animal to another.

The second theory, that of the effect of slight wind currents, can also be excluded, since the fireflies can be observed to flash on nights when there is absolutely no wind, and again on nights when there is a comparatively high wind. Likewise, Lund (14) has shown experimentally that the flashing of a firefly is in no way connected with the respiratory rhythm, or with the movement of the dorso-ventral abdominal muscles.

There is still one more theory which should be mentioned here, although it has not appeared in the literature on the synchronous flashing of fireflies. This theory assumes that the flashing of the insects is a mating adaptation. While this has been quite definitely proven to be the case with the forms found in Europe and America, there is no reason to believe that this explanation will fit conditions here. Among the Lampyridae the female is wingless and remains on the ground, or low shrubs, while the male flies overhead and flashes in response to the flash of the female. The *Soneratia* trees on which the animals congregate frequently grow in the water thereby preventing the female from coming near, and, furthermore, in all of the observations which the writer has made, he has never found a female either on the tree or in its vicinity.

A few paragraphs above it was said that there was an unlikelihood of there being a response on the part of the flies to any one particular animal. This is undoubtedly true once the synchronism has begun, but to say that it is not at all connected with such a phenomenon would be making a rather broad statement. On several

† By actual timing, the rate of the flashing is 120 per minute.

occasions it has been possible to inhibit the synchronism of a tree full of fireflies by turning a strong light on them for a half a minute. When flashing was again resumed it appeared to be quite irregular and then gradually assumed a rhythm, the leader, or leaders, being a closely grouped number of flies, the synchronism spreading from them in a wave until the entire tree was flashing in unison.

While this may serve as an explanation of the initiation of the process, there is still to be explained the fact that this synchronism, once begun, continues for long periods of time. It may be that the tree on which these animals are found has some effect which produces this remarkable phenomenon.

In Brandis' "Indian Trees" (15) one finds the statement that *Sonneratia* is a genus peculiar to the tropics of Asia, and, in fact, it is only from these tropics that this phenomenon has been reported. Whether there is something in the sap of the tree which attracts the animals and continues the synchronism in a manner somewhat similar to the rhythmical pulsation of an excised vertebrate skeletal muscle when placed in an isotonic salt solution, or whether the phenomenon is purely behavioristic are the questions to be answered.

A microscopic examination of the surface of the leaves of the *Sonneratia acida* brings to light the fact that they are well-supplied with openings. Aside from the usual stomata, there are present a large number of accessory structures, the "water stomata". The presence of these latter points to an excessive amount of water loss over the surface of the leaf. Furthermore, a complex carbohydrate which can be easily hydrolized has been detected in the sap of the tree, and it may be this substance which attracts the fireflies. In fact, the writer is inclined to look for an effect of the plant on the animals, rather than consider this phenomenon as purely behavioristic.

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